

THE MORPHOLOGY AND RELATIONSHIPS OF CERCIDIPHYLLUM

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With two plates and eight text-figures

INTRODUCTION

OF THE FIVE FORMERLY ASSOCIATED GENERA, *Trochodendron*, *Tetracentron*, *Euptelea*, *Cercidiphyllum* and *Eucommia*, the first three have recently been thoroughly re-investigated by A. C. Smith (29, 30), Bailey and Nast (3) and Nast and Bailey (24, 25). The totality of evidence from all organs and parts of these plants indicates that, although the vesselless genera *Trochodendron* and *Tetracentron* are related, they exhibit no close affinities either to *Euptelea* or to the Magnoliaceae (*sensu stricto*), Winteraceae, Illiciaceae, or Schisandraceae.

There has been much speculation regarding the relationships of *Cercidiphyllum*, and it is desirable that this genus also be re-examined from a broad morphological point of view.

LEAF: EXTERNAL FORM

One of the most conspicuous characteristics of *Cercidiphyllum japonicum* Sieb. et Zucc. is its dimorphic foliage, *Fig. 1*. The broadly cordate or reniform, palmately veined leaves with crenate margins, that are referred to in the generic name as Cercis-like, are borne on short shoots. On the contrary, the long shoots of the current year's growth bear leaves which fluctuate from elliptic to deltoid to broadly ovate and have entire or finely rounded-serrate margins. In leaves of the short shoots (*d-i*), the primary veins diverge from a single locus at the base of the leaf, whereas in leaves of the long shoots (*j-p*), they frequently diverge in pairs at successive levels. Although both kinds of leaves fluctuate considerably in size, the ranges of variability in form, venation, and character of the margin are much wider in the case of the leaves of the long shoots than in those of the short shoots. The leaves of seedlings have fewer marginal glands and therefore fewer and relatively much coarser appearing crenulations (*b-c*). The cotyledons are oblong-obtuse with entire margins (*a*).

Brown (5) has performed a highly significant paleobotanical task in re-investigating fossil floras and in demonstrating by the occurrence of associated fruits, seeds and leaves that *Cercidiphyllum* was widely distributed in the Northern Hemisphere during the Upper Cretaceous and Tertiary. The fossil leaves had previously been assigned to twenty-one different genera, including *Boehmeria*, *Ceanothus*, *Cercis*, *Cissus*, *Dombeyopsis*, *Ficus*, *Grewia*, *Hakea*, *Hedera*, *Paliurus*, *Piper*, *Populus*, *Smilax*, *Viburnum*, and *Zizyphus*, and the fruits and seeds to suggested relation-

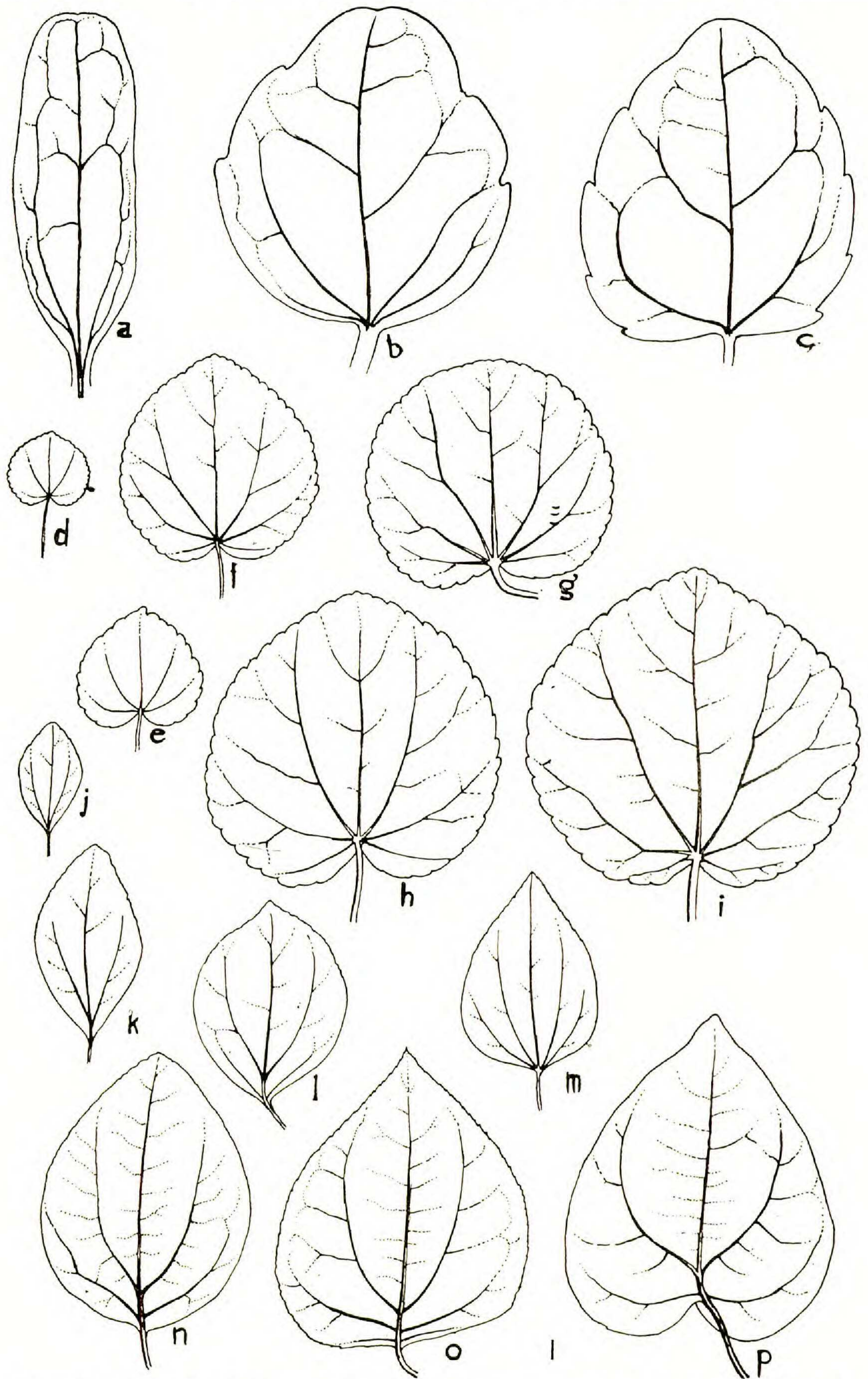


FIG. 1. a-c. Cotyledon and seedling leaves, *a*, $\times 7$, *b*, $\times 6$, *c*, $\times 5$. *d-i*. Outline tracings of the leaves of the short shoot, $\times \frac{1}{2}$. *j-p*. Same, of long shoot, $\times \frac{1}{2}$. In each figure, only the prominent veins are shown.

ships with such diversified plants as the conifers, palms, Leguminosae, Nyssaceae, Tiliaceae, Proteaceae, etc.

In view of the obvious polymorphism of the leaves of the surviving species of *Cercidiphyllum*, and in order to avoid overloading the literature with a host of fossil species based upon minor variations of leaf morphology, Brown recognized four fossil species based upon norms of foliar form; (1) elliptic to broad-ovate-elliptic with rounded or cuneate base in *C. ellipticum* (Newberry) Brown of the Upper Cretaceous and Paleocene, (2) deltoid with tendency to elongate apex and incipient cordate base in *C. arcticum* (Heer) Brown from the Paleocene to the middle Eocene, (3) elongate broad-lanceolate with cordate base in *C. elongatum* Brown from the middle or late Eocene to the upper Oligocene or lower Miocene and (4) cordate, slightly elongate and asymmetric in *C. crenatum* (Unger) Brown from the Oligocene to the late Miocene.

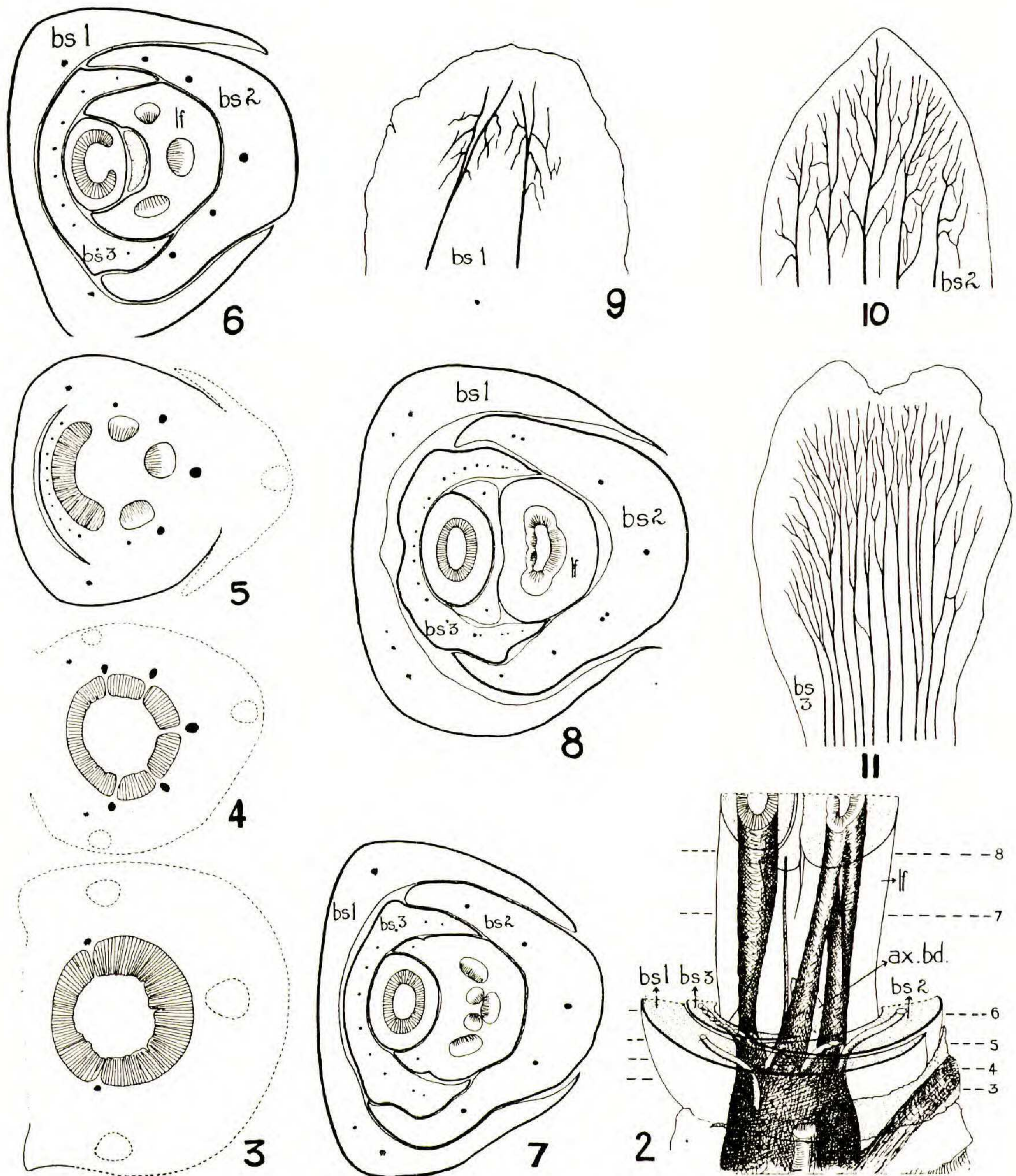
Although all five species of *Cercidiphyllum* exhibit wide ranges of foliar variability, it is evident that the frequency of occurrence of specific leaf forms changes in passing from the Upper Cretaceous *C. ellipticum* to the living *C. japonicum*. The broadly cordate leaves with crenate margins that Brown adopts as the norm of the latter species occur on the short shoots, whereas the leaves of the long shoots exhibit a much wider range of morphological variability which simulates that which occurs in the older fossil species. It appears likely that one of the extreme variant forms of the ancestral species may have stabilized on the short shoots of *C. japonicum* and possibly also of *C. crenatum*. This suggests that all of the leaves of *C. ellipticum* and *C. arcticum* may have been borne on long shoots. In any case, there are two norms of foliar form in *C. japonicum*, one characteristic of the short shoots and the other of the long shoots; the ratios of the two types of leaves fluctuating on a tree during successive parts of a growing season.

LEAF: VASCULATURE

Each of the cotyledons of *C. japonicum* is vascularized by two dichotomizing strands, the central branches of the dichotomies fusing to form the midvein of the cotyledon, *Fig. 1a*. The two strands are related to a single gap in the eustele of the cotyledonary node, *Fig. 55*. On the contrary, each of the paired primary leaves of the seedling is vascularized by three strands that are related to three separate gaps in the eustele, *Fig. 56*. The leaves of subsequently formed long shoots similarly are vascularized by three strands that are related to trilacunar nodes, *Fig. 57*. In contrast the leaves of the short shoots differ markedly in having three strands that are related to unilacunar nodes, *Figs. 5, 6*. The three strands behave similarly, however, in the petiole and lamina of leaves of both long and short shoots. In the basal part of the petiole two branches of the median strand pass* into an adaxial position with inverted orienta-

*The phraseologies used in this paper are descriptive of changes observed in successive serial sections and have no implications regarding ontogenetic or directional differentiation of the vascular elements.

tion of xylem and phloem, *Figs. 7 and 58*. These small strands with the three larger ones become aggregated into a vascular cylinder, *Figs. 8 and 59*, which extends throughout the central part of the petiole. Toward the base of the lamina, this vascular cylinder becomes invaginated on its adaxial side, *Fig. 60*, and gives rise to from five to seven U-shaped or concentric strands, *Figs. 61 and 62*, that constitute the primary veins of the palmate lamina.



FIGS. 2-11. *Fig. 2*. Diagrammatic reconstruction of the pattern of vasculature of a short shoot. *Figs. 3-8*. Transverse sections of the short shoot at levels as indicated by corresponding numbers in *Fig. 2*. *Figs. 9-11*. Drawings made from cleared preparations of the first, second and third bud scales to show the method of vascularization. (*bs1* — outermost bud scale; *bs2* — inner bud scale; *bs3* — innermost bud scale; *lf* — leaf; *ax. bd.* — axillary bud.)

LEAF: MISCELLANEOUS STRUCTURES

As observed and figured by Harms (13), there is a precocious development of concrescent stipules and large marginal glands even in leaf primordia that are still enclosed within the bud. As the leaf expands the adaxially oriented, conspicuously forked stipular appendage drops off and the glistening, hyaline glands abort, leaving more or less conspicuous depressions in the margin of the matured leaf. As noted by Solereder (31), the stomata are confined to the lower epidermis and are surrounded by from four to six ordinary epidermal cells. Rarely, however, one or two of the latter cells may undergo anticlinal division to form cells of smaller dimensions. The leaves do not contain secretory idioblasts or sclereids, nor do they form characteristic types of hairs or trichomes.

"FLOWER BUD" OF THE SHORT SHOOT

The bud of the sympodially elongating short shoot has three conspicuous reddish scales. The outermost of these (*bs1*) is connivent, viz. oriented with its dorsal side toward the main axis of the preceding year's growth, *Figs. 2, 6, and 8*. The second scale (*bs2*) is opposite the first and the third (*bs3*) in conformity with the first. A leaf (*lf*) with a bud (*ax bd*) in its axil forms opposite the innermost scale. The inflorescence is terminal. Thus, each year's elongation of the short shoot is produced by the activity of an axillary bud.

The outermost bud scale (*bs1*) contains two main veins that are related to two widely separated lacunae of the vascular cylinder, *Figs. 3-7*. These veins remain unbranched for some distance and then bifurcate, *Fig. 9*. Most of the branches arising from the veins tend to spread in a downward direction. The second bud scale (*bs2*) has five main veins that are associated with a corresponding number of lacunae, *Figs. 4-8*. The veins branch more or less profusely in the lamina and the branches anastomose forming a reticulate system, *Fig. 10*. The innermost bud scale (*bs3*) is supplied with from seven to eleven veins, arising from closely spaced but distinct lacunae, *Figs. 4-8*. The veins run parallel for a greater distance in the bud scale and then branch in a predominantly dichotomous manner, *Fig. 11*.

The parenchymatous tissue between the stelar bundles that alternate with those of the third bud scale soon become bridged by the activity of the cambium, and at a higher level the stele appears as a continuous arc on the adaxial side, *Fig. 5*. Conversely, on the side of the second bud scale, cambium fails to differentiate in the inter-fascicular regions excepting in the parenchyma flanking the median vein of the second bud scale. Thus, the vasculature on this side (right hand side in *Fig. 5*) becomes organized into three large strands. These enter the petiole, *Fig. 6*. It is evident, accordingly, that the three veins of the leaf of the short shoot are related to a single lacuna of the eustele in contrast to the nodal situation of the long shoot, where the three veins are related to three separate lacunae, *Figs. 56, 57*. The arc-shaped segment of the stele on the side of the third

bud scale soon becomes cylindrical, *Figs. 6, 7*, and continues into the reproductive axis.

THE FEMALE INFLORESCENCE

The reproductive axis is highly condensed and bears either carpels or stamens in conformity with the unisexuality of the plant. In the female inflorescence, the axis bears from two to six carpels, whose ventral sutures are characteristically directed away from the axis, *Figs. 12, 16*. At first sight the carpels seem to be aggregated in a cycle, but a careful examination reveals a more or less decussate arrangement, *Fig. 12*. Each carpel is subtended by a membranous bract. The relation of bracts to carpels is especially significant in those instances where more than four carpels are involved. As noted by Harms (13) and as is evident in *Fig. 20*, the bracts of the inner two "pairs" of carpels are distinct, originate at higher levels and do not represent parts of a single involucre.

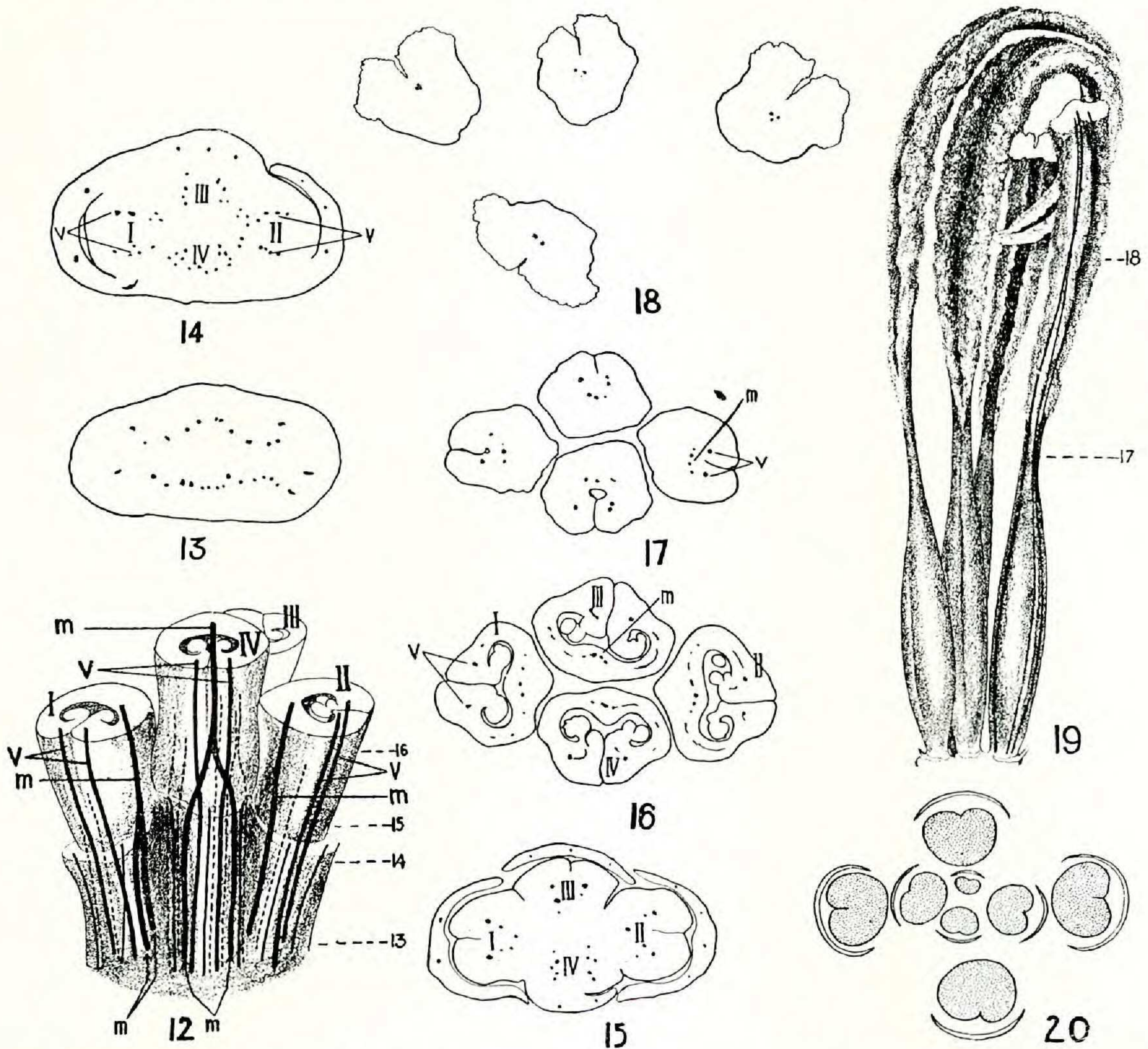
The shape, size and vascular supply of the bracts vary considerably. The bracts related to the outermost carpels generally are larger and more deeply lobed than those accompanying the inner carpels. The larger bracts usually receive three veins from the eustele of the reproductive axis, *Figs. 13, 14*; however, either the median or a lateral may be absent. The bracts subtending the inner carpels very rarely receive all three veins. Especially when the bracts are very much reduced, they may be unvascularized.

The carpel of *Cercidiphyllum* exhibits a particular trend of specialization of the primitive conduplicate megasporophyll* of the *Tasmania-Degeneria* type. It has acquired a much elongated form with a cylindrical ovule-bearing part and a long slender style having two extensively "decurrent" stigmatic ridges, *Fig. 19*. The external double stigmatic crests of the *Tasmania* type have been completely eliminated from the fertile part of the carpel, and the inner ventral surfaces beyond the placentae remain tightly adpressed, *Figs. 12, 16*, until dehiscence of the fruit. The stigmatic part of the carpel exhibits some flaring of the conduplicate surfaces, *Fig. 18*.

A reproductive axis bearing four carpels is illustrated in *Figs. 12-19*. After vascularization of the bracts, the bundles of the eustele resolve themselves into four groups, *Fig. 14 (i, ii, iii, iv)*. The peripherally situated bundles of each group (marked *v* in the figures) form the ventral veins of the corresponding carpels. The bundles that are situated towards the interior of the groups (marked *m* in the figures) give rise to the median vein. In the majority of cases, a single bundle from the stele departs into the carpel as its median vein, as in the carpel marked *ii* in the figures. Frequently, however, the median vein may be a fused product of two distinct stelar bundles, as in the carpels marked *i* and *iv* in the figures. Carpels exhibiting one or the other of these types of median veins fluctuate widely in distribution; some reproductive axes may have one type or both

*It seems wise to retain the terms megasporophyll and microsporophyll for descriptive purposes in dealing with the broader forms of angiospermic fertile appendages, without implications of their derivation from leaves.

types in varying proportions. A few of the remaining stelar bundles of each group disappear at the bases of the respective carpels, although some of these veins may occasionally traverse the tissue of the carpel for a short distance (such veins are indicated by broken lines in *Fig. 12*).



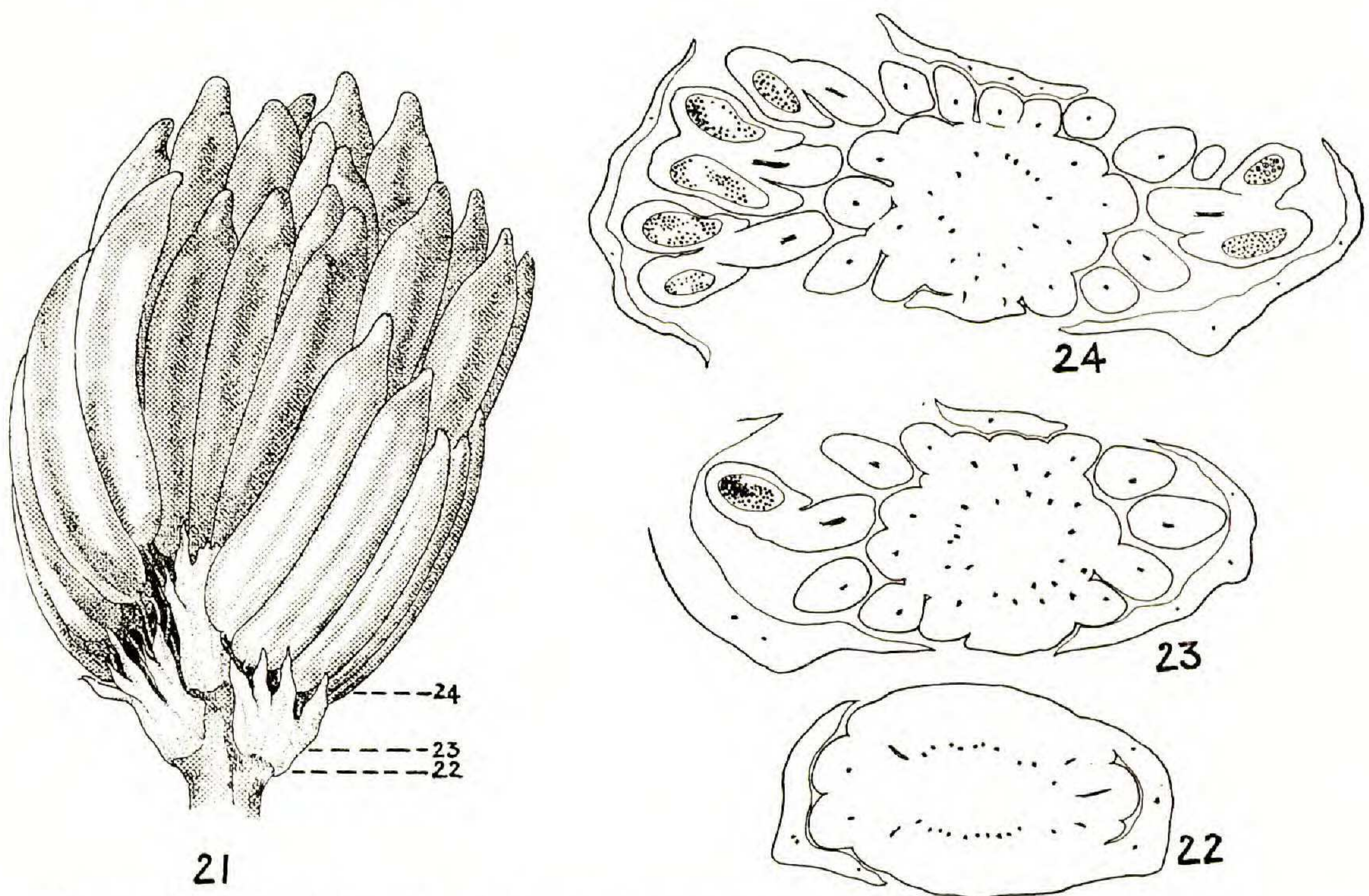
FIGS. 12-20. *Fig. 12.* Three-dimensional drawing of the vascular system of the female reproductive axis and carpels (vasculature of carpel marked III is not shown). *Figs. 13-18.* Transverse sections of the female reproductive axis and carpels as indicated by corresponding numbers in *Figs. 12* and *19*. *Fig. 19.* Four carpels from a reproductive axis, showing the general form. Vasculature is shown only for the carpel on the right-hand side. *Fig. 20.* An optical transverse section of a female reproductive axis bearing eight carpels, showing the relationship of the carpels and bracts. (*m* — median vein of the carpel; *v* — ventral vein).

It may be noted that generally a larger number of stelar bundles are aggregated below the ultimate carpel (number *iv* in the case illustrated in *Figs. 12, 14*). In addition to forming the median and ventral veins of the carpel, many of these bundles continue into the base of the carpellary wall (veins indicated by broken lines in carpel *iv*, *Fig. 12*). Within the carpel, the median vein gives off lateral branches that spread in the ovary

wall. The ventral veins, after vascularizing the ovules, extend upward in the style for more than half its length, *Fig. 17*; (also, carpel on the right hand side in *Fig. 19*).

THE MALE INFLORESCENCE

The male reproductive axis terminates in a cluster of stamens, subtended not infrequently by four membranous bracts corresponding to those associated with the carpels. It is important to note that the bracts tend to be arranged in opposite pairs on the reproductive axis, at slightly different levels and not in a truly cyclic manner, *Figs. 21, 22*. Furthermore, each bract appears to subtend an individual aggregation of stamens, the number of stamens in each aggregate varying from 8 to 13. The relation of the bract to the aggregation of stamens is particularly evident in the lower part of the axis, *Fig. 21*.



FIGS. 21-24. *Fig. 21*. Male reproductive axis. Note the arrangement of stamens in bunches, each bunch being related to a bract. *Figs. 22-24*. Transverse sections of the same from levels as marked by corresponding numbers in *Fig. 21*.

Although each bract in general is supplied with three vascular strands from the stele of the reproductive axis, the range of variation cited in connection with the bracts of the female reproductive axis is often encountered here also. After the vascularization of the bracts, the remaining bundles of the stele soon become centrifugally distributed, and each bundle supplies a single stamen, *Figs. 22-24*.

In the young condition, before the opening of the bud scales, the stamens have relatively long anthers and very short "filaments," *Fig. 21*. On the

contrary, at anthesis the "filaments" become greatly elongated and are nearly as long or even longer than the anthers. The "connective" is much reduced and the elongated sporangia are oriented in a latrose position. However, the microsporophyll broadens beyond the sporangial region forming a short conical apex. The staminal vascular bundle runs unbranched almost to the distal extremity of the stamen.

NATURE OF THE "FLOWERS"

As emphasized by Solereder (31) and subsequently by Harms (13), the abaxial orientation of the ventral sutures of the carpels in *Cercidiphyllum japonicum* is a serious, if not an insuperable, obstacle to interpreting the female reproductive structures as a single flower. A detailed study of successive stages in the development of carpels and fruits reveals no evidence of "twisting," Hutchinson (18), or resupination. Furthermore, the vascularization pattern of the reproductive parts negates any assumption of torsion or rotation. As previously indicated the ventral veins of the carpel are derived from bundles situated toward the periphery of the axis whereas the dorsal vein arises from a more centrally situated bundle or bundles, *Figs. 14, 15*. The decussate arrangement of paired carpels with their subtending bracts — particularly where six carpels are present — invalidates any interpretation of the bracts as parts of a single involucre, as noted by Harms (13).

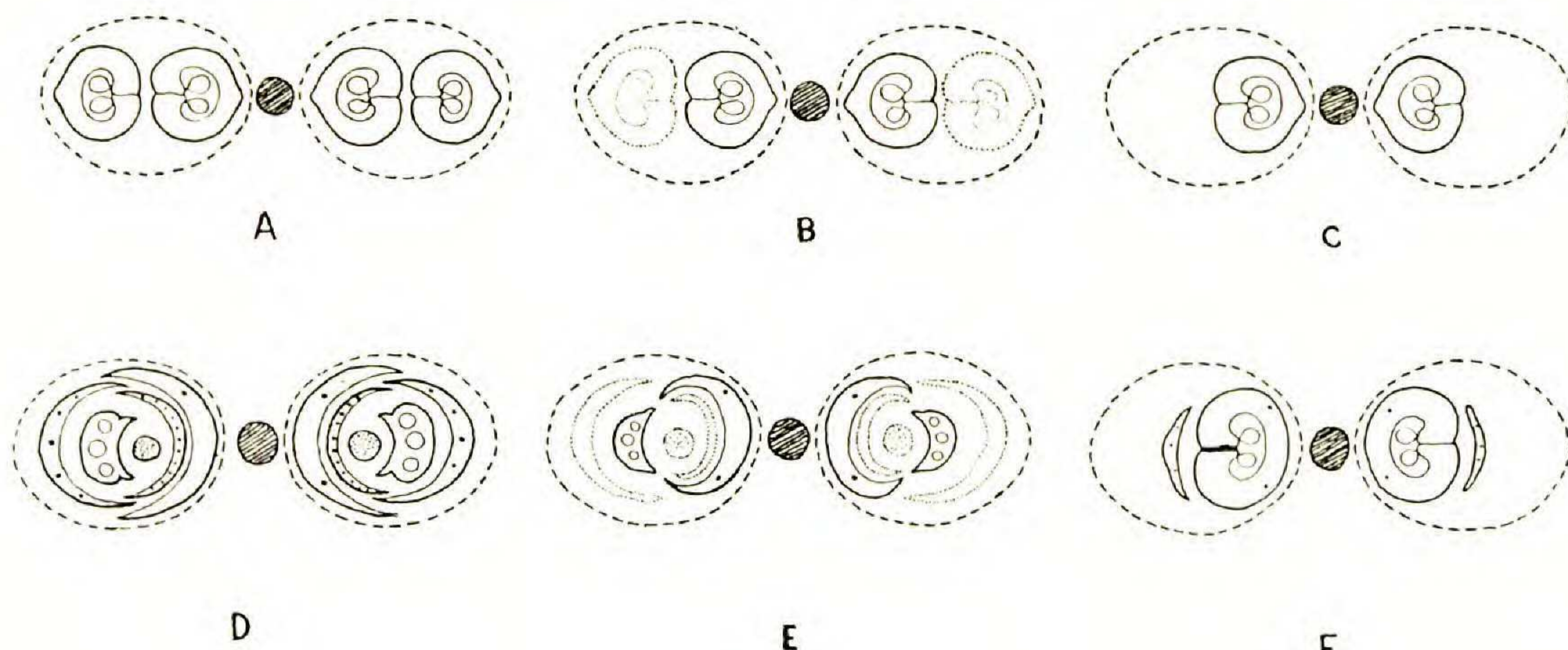
That the reproductive structures of *Cercidiphyllum japonicum* were actually derived by extreme reduction of an inflorescence is clearly demonstrated by paleobotanical evidence, Brown (5). In *Cercidiphyllum ellipticum*, *C. arcticum* and *C. elongatum* the fruits were borne on a much elongated axis and in the case of the first species on a branching inflorescence. Indeed, Brown concludes that "The fruits, at least in the early species, were borne in racemes, the individuals being indiscriminately alternate and opposite in the same raceme." Thus, each carpel of *C. japonicum* represents the vestige of a much reduced female flower and by homology each of the smaller aggregates of stamens with its subtending bract is the remains of a single male flower.

Two different trends in the reduction of the female flower to a single carpel with a subtending bract have been suggested by Solereder (31) and Harms (13). The two possibilities are graphically illustrated in *Fig. 25*. According to Solereder, the ancestral female flower of *Cercidiphyllum* might have possessed at least two carpels whose ventral sutures faced one another, *Fig. 25,A*. In each flower, the particular carpel which has its ventral suture adaxially oriented disappeared during subsequent evolution, *Fig. 25,B*, and the carpel which has its ventral suture abaxially oriented survived, *Fig. 25,C*.

On the contrary, Harms emphasized the similarity between the orientation of the carpel on the axis of the reduced inflorescence and that of the first bud scale on the vegetative axis. He hypothesized that the bud scale became fertile and transformed into a carpel and that the vegetative leaf

or its stipular appendage became the subtending bract of the carpel, *Fig. 25, D-F*.

Both of these suggestions are obviously highly speculative, but Solereder's concept is preferable owing to its directness and simplicity, involving merely loss of parts and not calling upon complex transformations of bud scales into carpels and of leaves into bracts. Unfortunately there are no reliable data available for thoroughly substantiating what actually occurred. Although the supernumerary bundles at the base of the carpels are indica-



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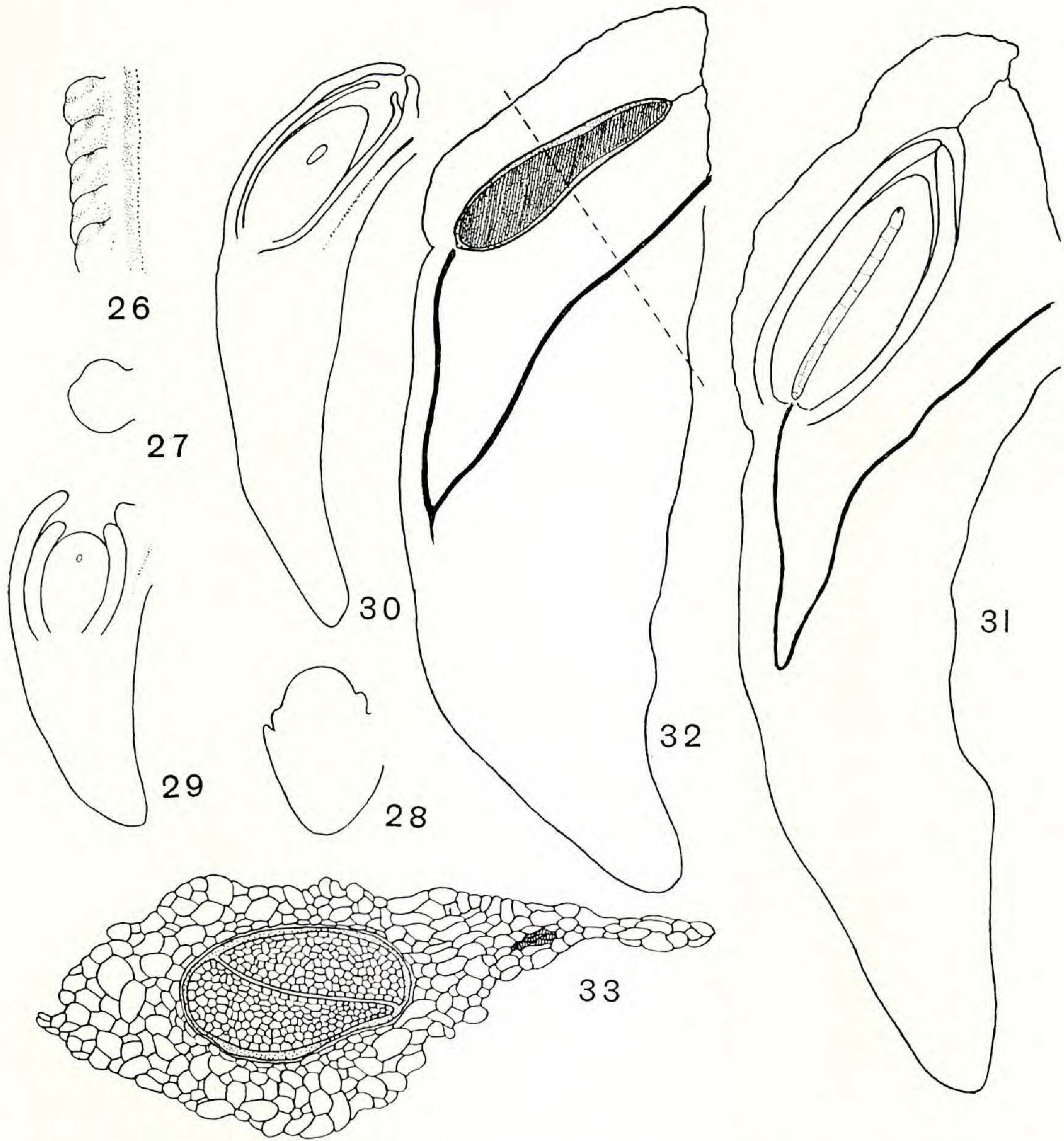
FIG. 25. Schematic representation of the two interpretations of the "flower" of *Cercidiphyllum*. A-C conveys Solereder's view and D-F, that of Harms.

tive of a loss of parts, reduction has progressed to a stage where it is impossible to determine with certainty the number and character of the appendages that may have been eliminated. Through the courtesy of Dr. Roland W. Brown, we have been able to examine the inflorescences of fossil species. Some of these bear paired carpels (fruits), but the preservation of the material is such (compressions and casts) that there is no conclusive evidence to indicate whether the ventral sutures of the paired carpels face one another or are oriented as in the much compressed inflorescence of *C. japonicum*. The discovery of favorably preserved material may clarify the issue.

EMBRYOLOGY

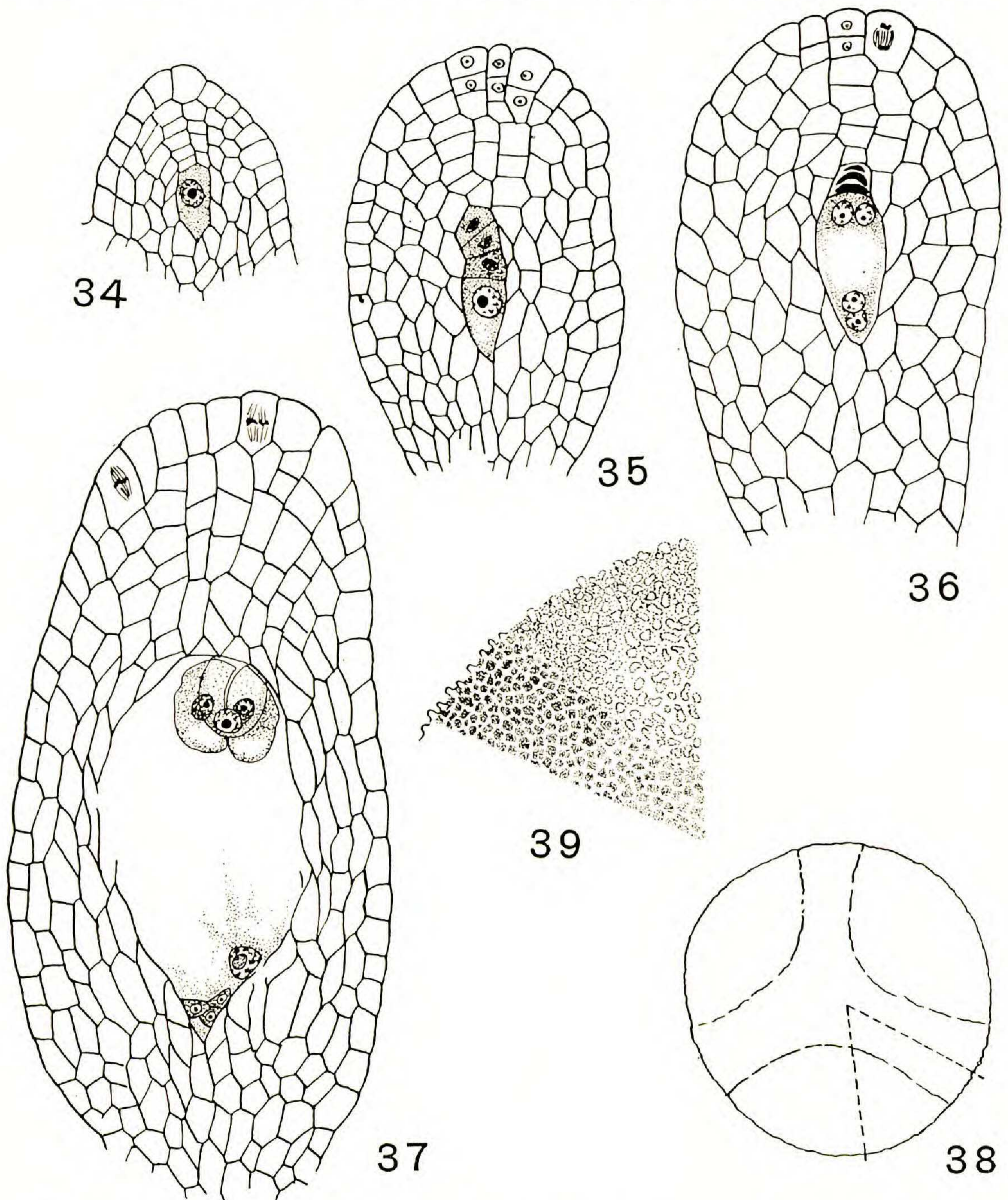
A single row of ovular primordia originates on each placenta. At first, the ovules appear as tiny knobs, *Fig. 26*, and even before the differentiation of the integuments, assume an orientation more or less parallel to the placenta, *Fig. 27*. During the development of the integuments, *Fig. 28*, the chalazal end of the ovule grows at a very rapid rate in the form of a flattened tapering projection, *Figs. 29-32*, which later develops into a wing. The differentiation of the vascular bundle in the ovule is rather late. The procambium of the bundle appears first in the funicular region, when the embryo sac is already in the 2- to 4-nucleate stage, *Fig. 29*. Even at the

time of fertilization, the procambium does not extend as far as the nucellus, nor have many of the constituent cells of the bundle become differentiated as spiral elements, *Fig. 30*. It is only after fertilization that the bundle undergoes a rapid and complete development. It first proceeds in the direction of the chalaza, and in the middle of the wing takes a circuitous course to reach the base of the nucellus, *Figs. 31, 32*.



FIGS. 26-33. *Fig. 26*. Ovular primordia on a placenta as seen in dissected preparations, $\times 70$. *Fig. 27*. Longitudinal section of an ovular primordium at a slightly later stage than in the previous figure, $\times 35$. *Fig. 28*. Same, at the time of the origin of integuments, $\times 35$. *Fig. 29*. Longitudinal section of an ovule when the megaspore mother cell is differentiating in the nucellus, $\times 35$. *Fig. 30*. Same, at the time of fertilization, $\times 35$. *Fig. 31*. Same, at an early stage in the formation of the endosperm, $\times 35$. *Fig. 32*. Longitudinal section of a mature seed, $\times 20$. *Fig. 33*. A section of the seed passing along the broken line in *Fig. 32*, $\times 70$.

The two integuments arise more or less simultaneously, *Fig. 28*. The outer integument grows beyond the inner, *Fig. 29*, and both the integuments take part in the construction of the micropyle, *Fig. 30*. The inner integument is from two to three layers of cells in thickness and the outer from four to five layers of cells at the time of anthesis. During subse-



FIGS. 34-39. *Fig. 34*. Longitudinal section of the nucellus showing the megaspore mother cell, $\times 240$. *Fig. 35*. Same, showing linear tetrad of megaspores, $\times 240$. *Fig. 36*. Same, showing 4-nucleate embryo sac, $\times 240$. *Fig. 37*. Same, showing mature embryo sac, $\times 240$. *Fig. 38*. Outline drawing of the polar view of a pollen grain, $\times 1500$. *Fig. 39*. Portion of the pollen grain, enclosed within the broken lines in *Fig. 38*, enlarged to show the sculpturing, $\times 3000$.

quent development, the inner integument becomes crushed and the outer one undergoes certain modifications which will be described in connection with the seed.

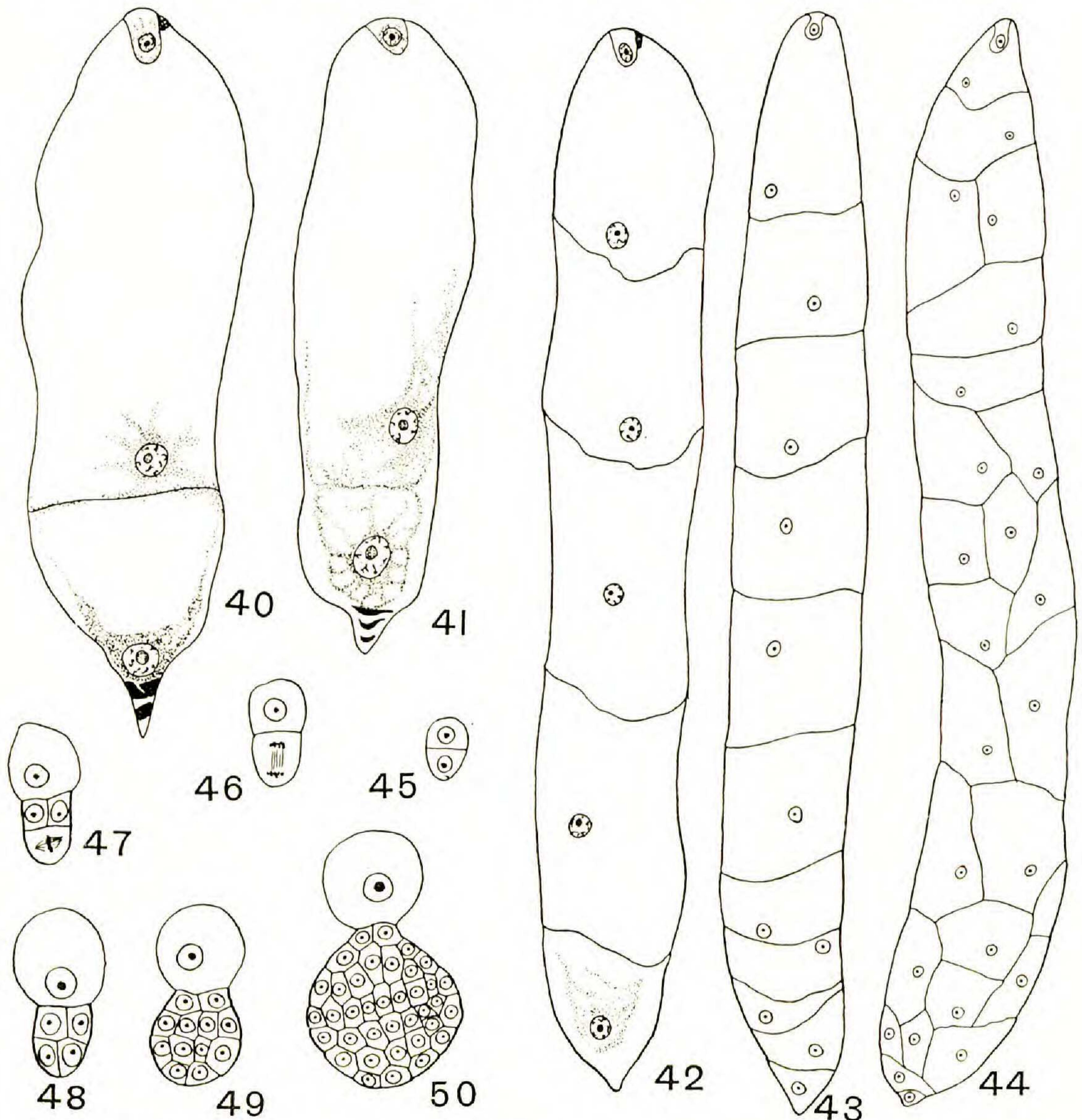
The primary archesporial cell differentiates in the hypodermal layer of the nucellus and divides by a periclinal wall into primary parietal and sporogenous cells. The former cell further divides in the same plane to give rise to from four to five parietal cells, *Fig. 34*. The epidermal cells capping the parietal tissue also undergo periclinal divisions to produce two or three additional layers that merge with the nucellus, *Figs. 35-37*. The sporogenous cell functions as the megaspore mother cell, *Fig. 34*. It divides meiotically to produce a linear tetrad of megaspores, *Fig. 35*, the chalazal megaspore further developing into the 8-nucleate embryo sac, *Figs. 36-37*. The antipodal nuclei organize into cells and the polar nuclei fuse before fertilization, *Fig. 37*.

The structure of the anther and the development of the male gametophyte do not deviate from the usual method known for the majority of dicotyledons. The anther tapetum is of the binucleate and secretory type. Microspore tetrads are formed by a simultaneous method of reduction divisions. After the formation of the vegetative and generative cells, the microspores are ready to be shed, and the division leading to the formation of the gametes takes place in the pollen tube.

The spherical and tricolpate pollen grains of *Cercidiphyllum* are very distinctive. The furrows are so broad that they occupy more than half the surface of the grain, *Fig. 38*. It frequently is difficult to determine where the furrows begin and where the exine ends. The exine is finely pitted. The floor of the furrow is flecked with minute granulations, *Fig. 39*.

After fertilization, the embryo sac expands in a direction parallel to the long axis of the ovule. The primary endosperm nucleus moves towards the chalazal end of the sac and divides; the division being followed by the deposition of a wall. As a result, the embryo sac becomes transversely partitioned into a larger micropylar chamber and a smaller chalazal cell, *Fig. 40*. The latter often shows a denser accumulation of cytoplasm with characteristic vacuolation, *Fig. 41*. However, by the time the upper chamber divides into four to six cells, *Fig. 42*, the cytoplasm of the chalazal cell thins down and the cell begins to divide. The early divisions in both the cells of the 2-celled endosperm, *Figs. 40, 41*, take place essentially by transverse walls until from two to twelve endosperm cells are formed, *Fig. 43*. Simultaneously with these divisions, the embryo sac undergoes considerable longitudinal stretching and presents a very much elongated structure as shown in *Figs. 42-44*; so that the antipodal end of the embryo sac comes in contact with the vascular bundle of the ovule, *Fig. 31*. Subsequent divisions in the endosperm cells take place in various oblique planes, *Fig. 44*, and finally produce a compact mass of nutritive tissue, a large proportion of which, however, is used up by the embryo.

The zygote divides only after the endosperm cells begin dividing in oblique planes, as represented in *Fig. 44*. The basal cell of the 2-celled proembryo, *Fig. 45*, does not divide further but undergoes conspicuous enlargement, *Figs. 47–50*. The terminal cell divides by a wall parallel to the first, *Fig. 46*, so that the proembryo now consists of a linear row of three cells. The next division in the two derivatives of the terminal cell



FIGS. 40–50. *Figs. 40–44*. Stages in the development of the endosperm, $\times 140$. *Figs. 45–50*. Stages in the development of the embryo, $\times 560$.

takes place by vertical walls, *Figs. 47, 48*. Subsequent divisions in these cells result in the quadrant and octant stages, which by further development give rise to the mature embryo. At the stage of dispersal of the seed, the embryo is well differentiated and possesses a long hypocotyl and two cotyledons that enclose the primary shoot apex. A few layers of endosperm cells may persist as remnants around the embryo, but are insignificant, *Figs. 32, 33*.

In the mature seed, the outer integument becomes slightly compressed in the plane of the flattened wing; therefore, the chalazal wing appears to be extended on either side of the seed, *Fig. 33*. In the chalazal region of the wing, the cells are unequally and variously enlarged so as to present a more or less spongy texture. The vascular bundle retains its downwardly projecting loop, *Fig. 32*.

SECONDARY XYLEM AND PHLOEM

The secondary xylem of *C. japonicum* has been described by a succession of investigators. Therefore, certain features only need be commented upon by us. The growth rings as seen in transverse sections of the wood, *Fig. 51*, are delimited by three to five layers of radially compressed imperforate tracheary elements. The thin-walled, angular vessels are diffusely scattered, but in some specimens those of the early-wood are conspicuously larger than those of the late-wood, *Fig. 51*. The vessel members are very long with extensively overlapping ends, indicative of their formation by a relatively primitive form of non-storied cambium. The "perforation plates" are scalariform with numerous slender bars, *Fig. 54*. The vessel members frequently extend beyond the perforated facets in the form of narrow tapered ends, having "tertiary" helical thickenings, *Fig. 54*. The intervacular pitting fluctuates between scalariform, transitional and opposite. The rays of the first-formed secondary xylem are closely spaced, longitudinally extensive and mostly uniseriate, but in passing outward radially soon develop biseriate parts, *Fig. 52*. The rays of the later formed wood are lower, more widely spaced and typically heterogeneous, *Fig. 53*. The ray-vessel pitting varies from scalariform to transitional to opposite. Relatively large crystals of calcium oxalate occur more or less sporadically in the erect cells of the heterogeneous rays. Xylem parenchyma is apotracheal, scanty, diffuse, and terminal. The imperforate tracheary cells have conspicuously bordered pits in both their radial and their tangential walls. Although the cambium, vessels and imperforate tracheary cells are of relatively primitive dicotyledonous types, the ray structure is of a form indicative of an advanced stage in the ontogenetic and phylogenetic reduction in width and height of the multiseriate rays, Barghoorn (2).

According to Solereder (31), the bark contains isolated strands of sclerenchyma. In old stems, however, the sclerenchyma of the secondary phloem occurs in the form of successive concentric bands of varying circumferential extension.

Among plant fossils from early Tertiary beds of East Greenland, is a fossil wood from Cape Dalton which was assigned to *Corylopsites groenlandicus* by Mathiesen (21). This wood closely resembles that of *Cercidiphyllum* and of certain species of *Corylopsis*. It bears evidences of crystals in its wood parenchyma and rays, and was referred to *Corylopsis* by Mathiesen owing to the absence of such crystals in wood of *Cercidiphyllum* examined by him. The abundance of leaves of *Cercidiphyllum*

in early Tertiary strata of northern lands suggests, as noted by Brown (5), that *Corylopsites groenlandicus* is in all probability the wood of *Cercidiphyllum*.

AFFINITIES OF CERCIDIPHYLLUM

Although the genus *Cercidiphyllum* was established by Siebold and Zuccarini in 1846, the plant *C. japonicum* remained without a specific name until Hoffman and Schultes (17) formalized its binomial, but no attempt was made to determine its affinities. In his remarks on the Hamamelidaceae, Baillon (1) casually raised the question whether *Cercidiphyllum* should be included under that family, noting foliar similarities with *Disanthus*. However, he also called attention to analogies with *Spiraeanthemum* of the Cunoniaceae (Saxifragaceae), viz. opposite leaves, hypogynous and apocarpous ovary and winged seeds. Maximowicz (22) associated *Cercidiphyllum* with *Trochodendron*, and particularly with *Euptelea*, in the Magnoliaceae, stressing the occurrence of stipules as evidence of relationship to that family.

Subsequent authors generally follow the lead of either Baillon or Maximowicz. Thus, Solereder (31), Hallier (8, 9, 10, 11), Lotsy (20), McLaughlin (23) and Croizat (6) emphasize similarities to the Hamamelidaceae, whereas Prantl (26), Harms (12, 13, 14), Bessey (4), Hayata (16), Hutchinson (18), Diels (7), Lemesle (19) and others favor retaining *Cercidiphyllum* within the Ranales (or Magnoliales) either as a member of the Magnoliaceae or the Trochodendraceae or as the representative of a monotypic family, the Cercidiphyllaceae.

The first comprehensive comparative studies of *Trochodendron*, *Tetracentron*, *Euptelea*, *Cercidiphyllum* and *Eucommia* (both of their external morphological characters and their internal structures) are those of Harms (12) and van Tieghem (33). Although cognizant of outstanding differences between the five genera, Harms, owing to an evident prejudice against small families, placed *Tetracentron* in the Magnoliaceae and the remaining four genera in the Trochodendraceae. On the contrary, van Tieghem, utilizing similar comparative evidence, placed each of the five genera in an independent family, grouping the monotypic Trochodendraceae and Tetracentraceae with the vesselless Winteraceae in a new order, the Homoxylées. It should be noted in this connection that Harms (13) later recognized the necessity of removing *Tetracentron* from the Magnoliaceae, of placing *Cercidiphyllum* in a family of its own within the Ranales and (15) of transferring the monotypic Eucommiaceae to the Urticales where Tippo's (34) subsequent investigations indicate that it in all probability belongs. Harms' (13) comments upon the taxonomist's difficulties in dealing with such genera as *Cercidiphyllum*, *Trochodendron* and *Tetracentron* are particularly significant. He states regarding *Cercidiphyllum*:

"On the whole the genus gives us many a problem; its morphological structure shows so many peculiarities that it is hard to find the correct place in the

system for the genus. But so it is with many other genera from eastern Asia. Often one does not know where to place these odd forms or to what more widely distributed and more richly developed families one should connect them. We may as well assume that these are old genera whose closer relations no longer exist. They are remainders of some more richly developed forms from former geological periods, now unknown to us, projecting into today's flora, in which they appear strange. Both the Japanese genus *Trochodendron* and *Tetracentron*, a genus growing with *Cercidiphyllum* in the mountains of central China and placed in the Magnoliaceae, where it does not belong, are isolated types."

This tendency among taxonomists and morphologists for gradually recognizing the necessity of segregating such relic genera in independent families of their own is in marked contrast to the highly speculative deductions of Hallier (11), who included *Trochodendron*, *Tetracentron*, *Euptelea*, *Cercidiphyllum* and *Eucommia* in the Hamamelidaceae along with the Balanopsidales, Batidales, Buxaceae, Geissolomataceae, *Daphniphyllum*, *Myrothamnus*, *Platanus* and other plants of doubtful affinities. Such a procedure stretches the family beyond the elastic limits of even a natural order.

Much of the confusion during the last fifty years in discussions of the angiosperms is due to the interjection of phylogenetic concepts into systems of classification that were not developed originally from an evolutionary point of view. The older systems are logical arrangements designed to facilitate accurate identification and to provide efficiency in the codification and use of specimens in large herbaria. The groupings of plants were primarily based upon morphological similarities in one or another of their parts. Modern attempts to arrange the larger groupings, viz. families and orders, in phylogenetic series, deriving one grouping directly from another, lead inevitably to increasing confusion and controversy. This is due to the fact that, in dealing with the survivors of very ancient angiospermic floras, such phylogenetic arrangements, based upon the study of specific selected parts of the plants, commonly are invalidated by evidence from other organs or parts of the same plants. The most that may be inferred from the *totality* of evidence from all organs and parts of the plants is, in a majority of cases, the conclusion that the related groups of plants were derived from common ancestors, now extinct. Furthermore, although *negations* of putative phylogenetic derivations are simple and conclusive, *positive* assertions regarding evolutionary derivations are difficult and uncertain owing to the common occurrence of parallel and convergent trends of morphological and anatomical specializations in all organs of the vascular plants. That similar end-products, resulting from such evolutionary trends, are of widespread and frequent occurrence among animals is becoming increasingly recognized by zoologists in dealing with both vertebrates and invertebrates.

Before attempting to arrange surviving angiosperms in phylogenetic series, it is essential to obtain reliable evidence regarding salient trends of evolutionary specialization in the various organs and internal structures of

these plants. Such evidence can be acquired only by comprehensive and time-consuming investigations of the dicotyledons and monocotyledons *as a whole*. In the case of the vascular tissues, accumulated data indicate that an adequate record of the derivation of vessels from modified tracheids and of the varied trends of specialization of vessel-containing xylem is preserved among both living dicotyledons and monocotyledons. However, it is evident from this record that similar or parallel trends of structural specialization have occurred repeatedly and independently in remotely related dicotyledonous families.

The voluminous data accumulated by successive generations of taxonomists provide abundant material for the study of varied trends of cohesion and adnation of floral parts and of simplification and reduction of inflorescences and flowers. Furthermore, the study of new and neglected plants from northern Australia, New Guinea, New Caledonia, Fiji and adjacent regions is yielding significant clues regarding the primitive form of the angiospermic carpel and stamen. Here again, as also in the case of angiospermic pollen, it is becoming increasingly evident that similar end products of specialization frequently develop independently through parallel or convergent evolution. Although much less is known at present regarding reliable trends of phylogenetic specialization in leaves and seeds of dicotyledons, sufficient evidence is available to indicate that morphological and structural similarities, *by themselves*, are not indicative necessarily of close genetic relationship between plants in which they occur.

Although specific parts of *Cercidiphyllum* exhibit similarities to homologous parts of other plants, the totality of evidence from all parts of the plants is not indicative of close relationship of *Cercidiphyllum* to any particular family of the dicotyledons. Many of the similarities stressed by those desirous of including *Cercidiphyllum* in the Magnoliaceae, Trochodendraceae or Hamamelidaceae are superficial and lose their significance when closely analyzed. Stipules, palmate venation, marginal glands and trilacunar nodal attachments of leaves occur in diverse families of dicotyledons, yet the presence of stipules is utilized by some as evidence of relationship to the Magnoliaceae and by others to the Hamamelidaceae. Similarly, stipules and palmate venation are stressed by some as indicative of affinity to *Tetracentron* and by others to certain selected genera of the Hamamelidaceae. It should be emphasized in this connection, however, that more detailed studies of the leaves reveal significant differences in the vasculature of the petioles and in the stomata of *Cercidiphyllum*. In addition, the leaves of this genus do not form types of idioblasts and other cellular structures that occur characteristically in the Magnoliaceae, *Tetracentron*, *Trochodendron* and various genera of the Hamamelidaceae.

Excessive emphasis has been placed in the past upon superficial resemblances due to analogous stages in the reduction of the perianth and other floral structures. In *Trochodendron* and *Tetracentron*, where the totality of evidence is clearly indicative of relatively close relationship between the two genera, the unsealed conduplicate carpels exhibit incipient lateral cohe-

sion, conspicuous nectariferous dorsal bulges and pronounced abaxial deformation either preceding or following anthesis. In contrast, the free, style-less carpels of *Euptelea* have elongated stipes and the stigmatic margins of the conduplicate megasporophyll are restricted by concrescence to a localized, more or less concave part of the ventral side of the carpel. In the Hamamelidaceae, as in many of the Cunoniaceae and Saxifragaceae, there is a marked tendency for the carpels to be reduced to pairs which have more or less extensive cohesion of their ventral surfaces. Thus, there are distinct and entirely different trends of specialization in the carpels of *Tetracentron* and *Trochodendron*, of *Euptelea*, and of the Hamamelidaceae, no evidence of which are detectable in the solitary carpel of *Cercidiphyllum*.

The pollen grains of *Tetracentron*, *Trochodendron* and certain of the Hamamelidaceae, as of many other dicotyledons, are tricolpate. Those of *Cercidiphyllum* are tricolpate, but differ markedly in the unusual breadth of their poorly defined furrows and in the detailed structure of their exine.

Embryological investigations have revealed no cogent evidence for including *Cercidiphyllum* in the Hamamelidaceae. The epidermal cells of the nucellus in *Cercidiphyllum* undergo a few periclinal divisions which result in an increased number of parietal layers, a phenomenon that has not been recorded in the Hamamelidaceae (27, 35). Following fertilization, the embryo sac of *Cercidiphyllum* undergoes a conspicuous elongation lengthwise, a feature which is unknown in the ovules of the Hamamelidaceae. The development of endosperm in *Hamamelis* (27), *Fothergilla* (35), and *Corylopsis* is strictly nuclear, whereas in *Cercidiphyllum* it is cellular.

The seeds of the Hamamelidaceae are of two different structural types: (1) those having a highly opaque, hard testa without wings, and (2) those that form a less opaque, relatively soft coat, whose margins become flattened to form a wing-like expansion. Seeds of the latter category are of less frequent occurrence in the family, being confined to the genera *Bucklandia*, *Liquidambar* and *Altingia*. The seeds of *Cercidiphyllum* are winged, but those who favor hamamelidaceous affinities for *Cercidiphyllum* have been too sanguine in citing this character as evidence in support of their contention. Winged seeds are of common occurrence and the presence of a wing in itself is not indicative necessarily of close relationship.

In the seeds of *Liquidambar* and *Altingia*, the outer integument surrounding the micropyle has undergone excessive flattening and considerable extension longitudinally to form the wing. The wing is radially symmetrical and its cells are uniform and more or less homogeneous. In *Bucklandia*, the histologically similar wing develops asymmetrically and diagonally from the outer integument on the side of the ovule opposite the raphe. There is no conspicuous extension of the chalazal end of the ovule or seed in these hamamelidaceous genera and the course of the raphe bundle is normal. On the contrary, the ovules of *Cercidiphyllum*

initiate the development of a subchalazal projection at an early stage of their ontogeny, viz. megaspore mother cell stage. Subsequent longitudinal and unilateral expansion of this subchalazal outgrowth forms the conspicuous wing of the mature seed. The raphe bundle forms a circuitous loop in the wing before reaching the chalaza, comparable to the hair-pin bend of the vascular bundle in the subchalazal prolongations of the ovules and seeds of *Trochodendron* and *Tetracentron*, Nast and Bailey (24).

The seeds of the latter genera, however, differ from those of *Cercidiphyllum* in having slender subchalazal elongations without broad wing-like modifications, in forming sclerenchymatous layers of characteristically elongated cells, and in containing a rudimentary embryo embedded in abundant endosperm. In addition, the epidermis of the outer integument consists of longitudinally elongated cells which impart a striated appearance to the seeds, whereas in *Cercidiphyllum* the homologous tissue is composed of cells which by enlargement produce a spongy texture.

The haploid number of chromosomes is commonly 12 in Hamamelidaceae. According to Whitaker (36), the haploid number is 14 in *Euptelea*, *Illicium* and the Schisandraceae, and 19 in *Cercidiphyllum*, *Trochodendron*, *Tetracentron*, the Winteraceae and the Magnoliaceae (*sensu stricto*). However, the occurrence of 14 haploid chromosomes in one investigated species of *Michelia* (32) suggests that many additional representatives of the Winteraceae, Magnoliaceae, Schisandraceae, and Illiciaceae should be studied before relying upon chromosome numbers in discussions of relationships within the Ranales.

The wood of *Cercidiphyllum* closely resembles that of certain representatives of the Hamamelidaceae, e.g. *Corylopsis*. However, this similarity, *by itself*, is not indicative necessarily of close relationship, since similar combinations of anatomical characters occur in other families which have retained relatively primitive cambia, vessels and imperforate tracheary cells while undergoing analogous reductions in the width and height of their multiseriate rays. In fact, the similarities in the case of *Corylopsis* and *Cercidiphyllum* are no more remarkable than are those between the woods of such remotely related plants as *Maclura pomifera* (Raf.) Schneid. of the Moraceae and *Robinia pseudoacacia* L. of the Leguminosae.

Thus, a summation of evidence from all organs and parts of *Cercidiphyllum* provides no cogent arguments for including this genus in any particular family of the dicotyledons. Therefore, we agree with van Tieghem (33) and subsequent writers who place the genus in an independent family of its own, the Cercidiphyllaceae.

Having established an increasing number of new independent families, taxonomists are faced with the problem of incorporating them in some logical and useful major system of classification. The role of the morphologist, anatomist, paleobotanist or cytogeneticist should be to provide significant and helpful data rather than to attempt to dictate solutions of this difficult problem upon their own terms. As previously stated, premature efforts to arrange living angiosperms in putative phylogenetic series,

deriving one family or order directly from another (Hallier and others) will lead only to increasing confusion and controversy. The study of major trends of phylogenetic modification of specific organs or parts of the dicotyledons and monocotyledons is yielding much significant information, but it should be recognized that no single one of these phylogenies can be utilized by itself in arranging plants in a similar linear series, since such a procedure is usually negated by evolutionary trends in other parts of the plants.

The Ranales, as broadly conceived by Engler and Prantl, obviously associates plants of widely varying degrees of relationship and of morphological and anatomical specialization. Two different categories of families may be recognized to advantage within the order: (1) the Winteraceae, Degeneriaceae, Magnoliaceae (*sensu stricto*), Himantandraceae, Eupomatiaceae, Annonaceae, Myristicaceae, Canellaceae, Calycanthaceae, Austrobaileyaceae, Monimiaceae, Gomortegaceae, Lauraceae, Hernandiaceae and Lactoridaceae, having characteristic secretory cells ("ethereal oil cells") and monocolpate pollen (or phylogenetically modified types of such pollen), and (2) the Ranunculaceae, Berberidaceae, Lardizabalaceae and Menispermaceae, having tricolpate pollen (or types derived from such pollen) and no "ethereal oil cells." Monocolpate pollen occurs in many seed ferns, Bennettitales, Cycadales, Ginkgoales and monocotyledons, whereas tricolpate pollen and its modifications characterizes most dicotyledons.

The plants of the first ranalian category are predominantly woody (normal trees and shrubs), having simple pinnately veined leaves (except the Hernandiaceae), syndetocheilic-appearing stomata, and seeds with copious endosperm and rudimentary embryos. They retain many early trends in the differentiation of sepals and petals and in the specialization of primitive conduplicate, unsealed carpels, broad microsporophylls and staminodes, as well as of vessels and other vascular structures. The second category of ranalian plants exhibits conspicuous trends toward the acquisition of herbaceous or scandent habits, have a high ratio of palmate venation, and form haplocheilic stomata. Although predominantly apocarpous, their flowers have in general attained advanced stages of modification, and their vascular tissues are highly specialized. However, they retain seeds with abundant endosperm and small embryos.

The Illiciaceae and Schisandraceae have abundant "ethereal oil cells" and other characters suggestive of the first category of Ranales, but form tricolpate or hexacolpate pollen. Furthermore, the Schisandraceae, as certain of the Monimiaceae and Hernandiaceae, exhibit transitions between syndetocheilic-appearing stomata and haplocheilic stomata. Conversely, the Nymphaeaceae are in general more nearly comparable to plants in the sub-order Ranunculineae, but the Cabomboideae and Nymphaeoidae have monocolpate types of pollen, whereas the Nelumbonoideae form tricolpate ones. It should be noted, in this connection, that although the Piperaceae and Saururaceae have attained a high degree of morphological specialization in most of their parts, they contain characteristic "ethereal oil cells"

and have monocolpate pollen. They should be included in the Ranales, if this order is to be retained as broadly conceived of in the Englerian system.

The Tetracentraceae, Trochodendraceae (*sensu stricto*), Eupteleaceae and Cercidiphyllaceae have tricolpate pollen, haplocheilic stomata and, with the exception of *Tetracentron*, no secretory idioblasts. If these families are to be retained in the Ranales, it should not be upon unwarranted assumptions that they are closely related to, or directly derived from the Winteraceae, Magnoliaceae, or any other specific family of the order, but rather upon recognition of the order as a useful repository for relic plants that retain primitive, ancestral, dicotyledonous characters in one or more of their organs or parts. Nothing is to be gained by transferring such genera as *Tetracentron*, *Trochodendron*, *Euptelea*, and *Cercidiphyllum* into close relationship with the Hamamelidaceae or Saxifragaceae, since this would merely serve to expand another order into a less homogeneous assemblage. The only other alternatives are to include each relic genus in a special order of its own or to follow the lead of mycologists and establish a special assemblage, e.g. "Incognitales," comparable to the Fungi Imperfecti.

It should be emphasized in conclusion that much of the present confusion in literature dealing with the relationships and phylogeny of angiosperms is due to premature and unduly speculative generalization based upon excessively restricted and inadequate data. A much broader outlook is needed, involving the use of evidence from all organs and parts of plants and an accurate visualization of salient trends of specialization of such organs and parts in the angiosperms, and in the vascular plants, as a whole.

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EXPLANATION OF PLATES

Plate I. *Fig. 51*. Transverse section of the mature wood, $\times 120$. *Fig. 52*. Tangential section near the early secondary xylem, $\times 120$. *Fig. 53*. Same, old secondary xylem, $\times 120$. *Fig. 54*. Part of a vessel member showing the spiral thickenings in the tapering end, $\times 320$.

Plate II. *Fig. 55*. Transverse section of a seedling at the cotyledonary node, $\times 40$. *Fig. 56*. Same, at the next node, $\times 40$. *Fig. 57*. Transverse section at the node of a twig, $\times 10$. *Figs. 58–60*. Transverse sections of the petiole at successive levels starting from the base, $\times 18$. *Fig. 61*. Transverse section passing through the base of the lamina, $\times 18$. *Fig. 62*. Same, at a slightly higher level, $\times 18$.

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